

Note on the terminal nerve in chimaeroid fishes (Holocephali; Chimaeridae)

by

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ABSTRACT. - William Locy in 1905 on page 63 of his morphological and embryological account “On a newly recognized nerve connected to the fore-brain of selachians” mentions the “new nerve” or “supernumerary nerve” as it was termed before that time, tentatively traced upon dissection of the brain of *Chimaera monstrosa*. The terminal nerve as designated by Locy has never been mentioned for holocephalan fishes since, though new interest arose more recently with description of the terminal nerve in a variety of vertebrates ranging from cyclostomes to man. This study fills a gap in our anatomical knowledge and describes the nervus terminalis in juvenile spotted ratfish (*Hydrolagus colliei*) and rabbit fish (*Chimaera monstrosa*) on the basis of whole-stained and serially sectioned specimens.

RÉSUMÉ. - Description du nerf terminal de deux chimères (Holocephali; Chimaeridae).

En 1905, William Locy mentionne à la page 63 de son article “On a newly recognized nerve connected to the fore-brain of selachians” le “nerf nouveau” ou “nerf surnuméraire”, comme il était dénommé auparavant, d’après une observation faite lors d’une dissection du cerveau de *Chimaera monstrosa*. Depuis, le nerf terminal, tel qu’il fut alors désigné par Locy, n’a jamais plus été signalé pour les holocéphales, malgré un regain d’intérêt récent dans ce domaine, avec la description du nerf terminal chez divers vertébrés, des cyclostomes à l’homme. La présente étude comble un vide dans nos connaissances anatomiques en décrivant le nervus terminalis chez des juvéniles de chimère tachetée (*Hydrolagus colliei*) et de rat de mer (*Chimaera monstrosa*) à partir de spécimens colorés et de coupes sériées.

Key words. - Chimaeridae - *Hydrolagus colliei* - *Chimaera monstrosa* - Nervus terminalis - Nervus olfactorius - Olfactory epithelium - Forebrain - Neuroanatomy.

The holocephalan or chimaeroid fishes, which have a long phylogenetic history, are often the focus of research by evolutionary biologists. During the last two centuries some research has been done on the morphology and phylogeny of the Chimaeriformes. In most cases the chimaeroid fishes are considered closely related to the Elasmobranchii and are widely considered to belong to a monophyletic Chondrichthyes (e.g. Schaeffer and Williams, 1977; Schaeffer, 1981; Zangerl, 1981; Maisey, 1986). Much work has concentrated on the cranium of chimaeroids (e.g. Leydig, 1851; Hubrecht, 1877; Garman, 1888; Cole, 1896a, 1896b, 1896c; Dean, 1906, 1909; Luther, 1909; Allis, 1917, 1926; Kesteven, 1933; De Beer and Moy-Thomas, 1935; Stahl, 1967; Didier, 1995). The characters investigated in most cases concern skeletal or muscular structure alone. Few investigations have been done on the cranial nerves. Only Cole (1896c) and Liu (2001) provide comprehensive studies on the cranial nerves of several holocephalans. The latter author describes and compares the cranial nerves of three species, *Callorhynchus callorhynchus* (Linnaeus, 1758), *Hydrolagus colliei* (Lay & Bennett, 1839), and *Harriotta raleighana* Goode & Bean, 1895, which cover all three holocephalan families. The terminal nerve has not

been described in detail for holocephalans and Liu (2001) even states that the terminal nerve is not present in the species he examined. This is particularly surprising considering that this nerve is present and particularly prominent in the Elasmobranchii, with an easily identified extracerebral fibre tract, in the closest extant relatives of the holocephalans (e.g. Locy, 1899, 1905; Norris and Hughes, 1920; Demski *et al.*, 1987).

What is this supernumerary nerve? It is rather incidentally mentioned and figured by Fritsch (1878), later detected by Pinkus (1895) in the lungfish *Protopterus*, by Allis (1897) in the actinopterygian *Amia*, by Locy (1899, 1905) in a multitude of elasmobranchs, by Serwertzoff (1902) in embryos and larvae of *Neoceratodus forsteri* (Krefft, 1870), and later, with refined technique, demonstrated in virtually all vertebrates (see Demski and Schwanzel-Fukuda (1987) for survey). Topographically closely related to or even intermingled with the olfactory nerve or the vomeronasal components of Jacobson’s organ in tetrapods, it connects the olfactory placode peripherally with the lamina terminalis or neuropore region, the embryonic anterior end of the neural tube of the telencephalon, centrally. Bi- and multipolar ganglionic cells

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may form a macroscopically more or less prominent, multiple or diffuse ganglionic component. From the ontogenetic studies in lower vertebrates, it seems that the terminal nerve emerges as a primary, ganglionated nerve of the olfactory placode with the ganglionic nerve cell components derived from this specialized sensory placode (Bartsch, 1993). Still the similarity with the autonomic nervous system may be in conflict with this view. Here we demonstrate a ganglionated terminal nerve, well separated from the fibre bundles of the olfactory nerve and tract in the holocephalans *Hydrolagus colliei* (Lay & Bennett, 1839) and *Chimaera monstrosa* Linnaeus, 1758.

MATERIAL AND METHODS

The basis of this study are histological transverse section series of *Hydrolagus colliei* (ZMB 33793) from the North Pacific (Oregon) and *Chimaera monstrosa* of the embryological collection of the ZMB, Bolk, Series A. Both section series are based on Paraffin embedded heads of juvenile individuals that have been cut into ten-micrometre thick sections. A Leica DME microscope was used for examination of the sections. Photographs were taken with a Zeiss AxioCam MRc 5. As a complement to this analysis the brains of three adult *C. monstrosa* and one adult *H. colliei* have been prepared and examined. Two whole cleared and stained juvenile specimens of *Hydrolagus colliei* (ZMB 33982, 33983) from the North Pacific coast of Washington State were used in addition for the comparison, course and orientation of major cranial nerve components (Fig. 1). These were prepared according to the combined methods of Dingerkus and Uhler (1977), Filipinski and Wilson (1984), and Taylor and van Dyke (1985). The musculature was digested by trypsin and the specimens immersed in glycerin. Sudan black was used for nerve stain, Alcian blue for cartilage and alizarin red for bone. Study material is deposited at the Museum für Naturkunde Berlin (ZMB).

RESULTS AND DISCUSSION

The tractus and bulbus olfactorius are the most anterior parts of the brain and reach about halfway above the nasal capsule and sac anteriorly. These are roofed over by cartilage of the anterior endocranium confluent with the nasal capsules. The tractus and bulbus olfactorius are relatively short in *Chimaera* and *Hydrolagus* in comparison with other chimaeroids (Liu, 2001). Corresponding with the position of the nasal sacs close to the midline, the tractus olfactorii do not diverge much anteriorly, as is usually the case in Elasmobranchii. The fibre bundles of the olfactory nerve enter the cranial cavity through a purely membranous wall, i.e. an unchondrified part of the roof of the nasal capsule. The nerve

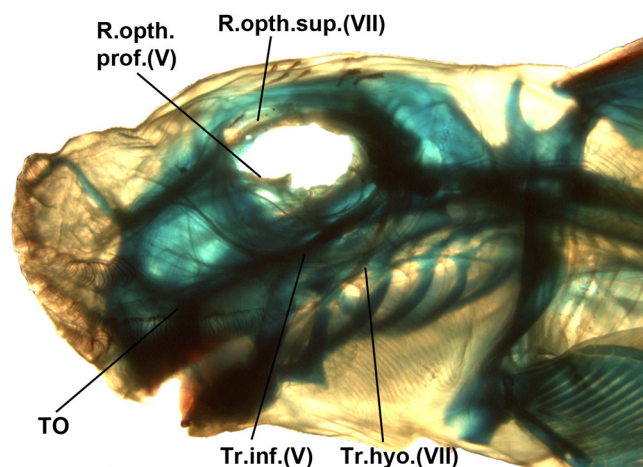


Figure 1. - A juvenile *Hydrolagus colliei* (ZMB 33982, 137 mm TL) whole-mount cleared and stained for cartilage (blue), calcifications, bone (red), and nerves (black) showing the general disposition of the central nervous system. R. oph. prof.(V): ramus ophthalmicus profundus; R. oph. sup.(VII): ramus ophthalmicus superficialis; TO: tractus olfactorius; Tr. hyo.(VII): truncus hyomandibularis; Tr. inf.(V): truncus infraorbitalis.

lies above the olfactory epithelium, mainly in a median raphe of connective tissue and enlarges as it gathers more and more small nerve branches posteriorly. Larger bundles of olfactory axons also enter the olfactory bulb directly from the lateral aspect of the nasal sac (Fig. 2A). The bulbus olfactorius continues into a short tract which enter the hemispheres of the telencephalon in an externally rather indistinct transition (Fig. 2B). The nervus terminalis (0) has its anterior origin at the olfactory epithelium and nasal capsule in the region of the anteriormost fibres of the nervus olfactorius (I). Its anterior ganglion lies on the inner ventral side of the first cranial nerve close to the nasal septum and sends afferent branches to the nervus olfactorius and/or close to the olfactory epithelium (Fig. 2A, B). The relative position of the nerve does not change following its course along the olfactory nerve posteriorly towards the bulbus and tractus olfactorius (Fig. 2C, D). A second ganglion is situated at the medio-ventral part of the telencephalic hemisphere (Fig 2E, F). Finally, the nervus terminalis enters the telencephalon medio-dorsally (Fig. 2E). During its course, the terminal nerve is closely associated with blood vessels (Fig. 2B, D).

In his study on the brain and cranial nerves of chimaeroid fishes, Liu (2001) states that the terminal nerve is not present in modern holocephalans. It is generally known that the terminal nerve is present in elasmobranch fishes (e.g. Locy, 1905; Johnston, 1911; Norris and Hughes, 1920), which are the closest extant relatives of chimaeroids. The terminal nerves in *Hydrolagus colliei* and *Chimaera monstrosa*, examined in this study, differ in their course from elasmobranchs. In the latter the terminal nerve rests on the rostro-dorsal surface of the olfactory bulb and runs dorsal or medial to the bulbus olfactorius and tractus olfactorius (e.g. Locy,

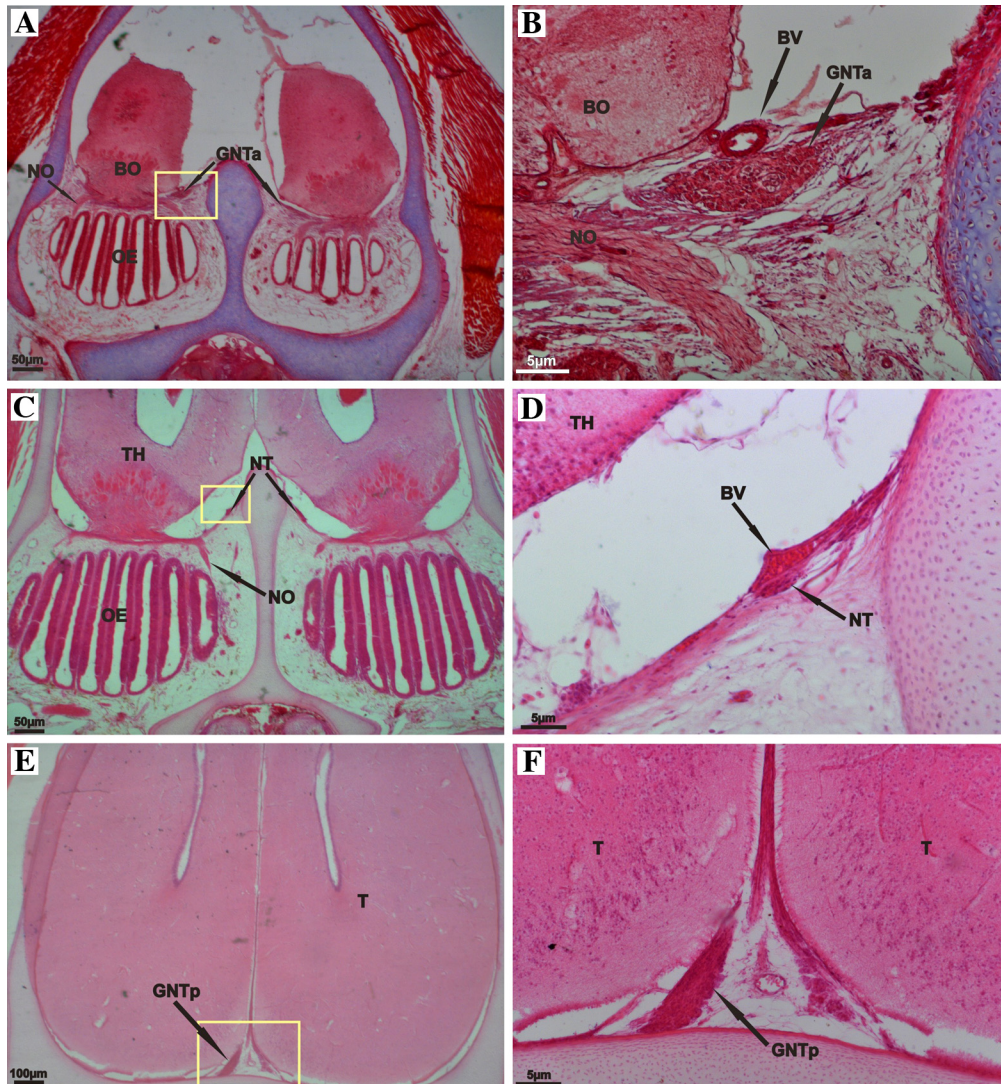


Figure 2. - Histological transverse sections through nasal sac and forebrain of hatchlings of *Hydrolagus colliei* and *Chimaera monstrosa*, respectively. The rectangles show the areas of enlargement. **A:** Anterior ganglion of the nervus terminalis, close to the olfactory epithelium and nasal capsule in the region of the anteriormost fibers of the nervus olfactorius in *Hydrolagus colliei* (ZMB 33793, 171 mm TL, North Pacific, Oregon). **B:** Larger magnification of squared regions in figure 2A. **C:** Relative position of the terminal nerve close to the nasal septum on its course posterior along the bulbous and tractus olfactorius in *Chimaera monstrosa* (Embryological collection of the ZMB, Bolk, Series A). **D:** Larger magnification of squared regions in figure 2C. **E:** Posterior ganglion of the nervus terminalis at the medio-ventral part of the telencephalon in *Chimaera monstrosa* (Embryological collection of the ZMB, Bolk, Series A). **F:** Larger magnification of squared regions in figure 2E. BO: bulbous olfactorius; BV: blood vessel; GNTa: anterior terminal ganglion; GNTp: posterior terminal ganglion; T: telencephalon; NO: nervus olfactorius; NT: nervus terminalis; OE: olfactory epithelium; TH: telencephalic hemisphere.

1905; Demski, 1987), whereas in the examined chimaeroids the terminal nerve has its entire course ventral and medial to the bulbous and tractus olfactorius (Fig. 3).

In basal osteichthyans the nervus terminalis usually is positioned ventrally of the olfactory tract and bulb for most of its course as shown in Allis (1897, Plate XXXVIII, Fig. 64). In Dipnoi and dipnoan larvae, however, in its distal part it is situated more dorsally, as shown in Pinkus (1895) and Bartsch (1993) and thus more similar to the elasmobranch condition.

Although the cranial nerves of chimaeroids have often

been examined the terminal nerve was not included in these studies. This is especially surprising because many of these studies were carried out when the nervus terminalis was new to science and the field of comparative functional neuro-anatomy of vertebrates was an active new area of research. Though extensively referring to the chondrichthyan fore-brain and with suitable material at hand, neither Johnston (1910, 1911) nor Nieuwenhuys *et al.* (1998) address the terminal nerve in Holocephali. We suspect that its unusual course in Holocephali might also have misled Liu (2001).

In our study we describe the nervus terminalis from two

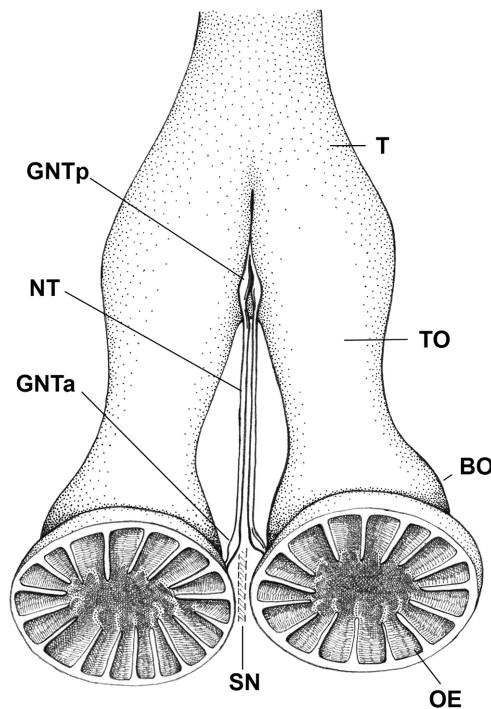


Figure 3. - Drawing of the forebrain and course of the terminal nerve in a dissected specimen of *Chimaera monstrosa* – ventral view. BO: bulbus olfactorius; GNTa: anterior terminal ganglion; GNTp: posterior terminal ganglion; NT: nervus terminalis; OE: olfactory epithelium/section of nasal sac; SN: septum nasi; T: telencephalon; TO: tractus olfactorius.

genera (*Chimaera* and *Hydrolagus*) belonging to one of the three families of modern holocephalans. It is still not confirmed from the material presently available to us, whether this nerve is also present in Callorhynchidae and Rhinochimaeridae. Even Schauinsland (1903) apparently missed it in his otherwise very informative 3-D reconstruction of the brain of *Callorhynchus milii*. It would be particularly interesting if the pattern of the nervus terminalis in Callorhynchidae (the most basal holocephalan family), is similar to that in Chimaeridae (i.e. an entirely ventro-mesial position relative to the bulbus and tractus olfactorius), or shows a more dorsal course as in elasmobranchs. However, in selachians the point of origin of the terminal nerve at the telencephalon medium and its distal course are somewhat variable (Johnston, 1911).

The terminal nerve is present in all major groups of vertebrates ranging from cyclostomes to man and accumulating evidence suggests a function in the context of reproduction, pheromone detection and the Luteinizing Hormone-Releasing Hormone System (e.g. Demski and Schwanzel-Fukuda, 1987; Bartheld *et al.*, 1987). The potential phylogenetic and developmental implications of its presence and course in holocephalans are yet to be determined, but our findings confirm the idea that the terminal nerve is a basic gnathos-

tome or vertebrate character. This study may thus trigger new questions and interest in the comparative anatomical, embryological, and functional study of this structure in vertebrates.

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